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THE TRANSITION FROM FUNGUS-FEEDING TO PLANT-FEEDING IN CECIDOMYIIDAE (DIPTERA)

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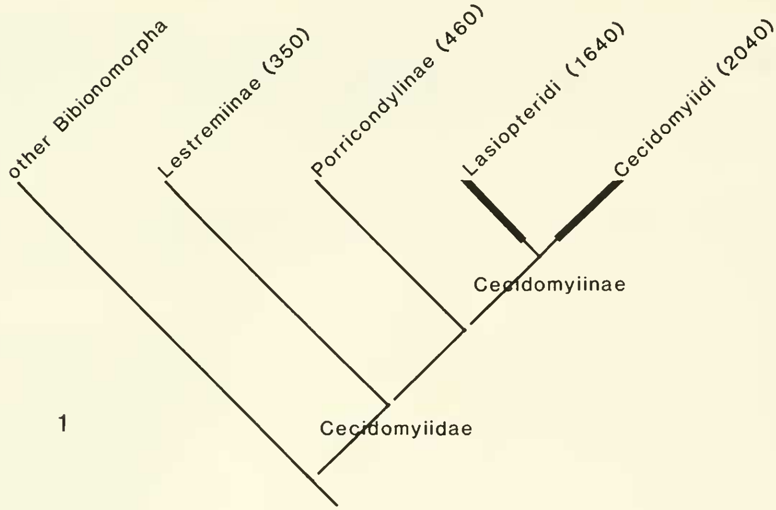
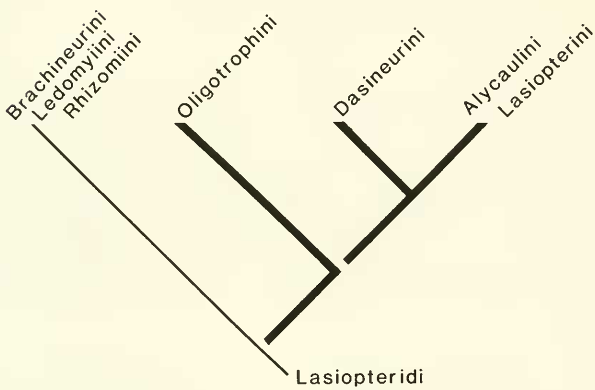
Abstract.—A speculative inquiry is made into the change in Cecidomyiidae from the ancestral fungus-feeding habit to the plant-feeding habit. Plant-feeding in these insects has apparently evolved separately at least three times. The greatest change necessary in switching to plant-feeding was in the salivary secretions, which cause the plant to react by producing food and gall tissue. Anatomical modifications needed for sucking plant juices and digging into soil were already present in fungus-feeding cecidomyiids and preadapted them for plant-feeding.

Enough is known about Cecidomyiidae to sketch a broad evolutionary outline of its groups and their relationships (Fig. 1). Primitive cecidomyiids are fungus-feeders and evolved from fungus-feeding land midges. Plant-feeding is a relatively recent habit in Cecidomyiidae and has probably developed separately in the family at least three times (Figs. 2–3). Where that habit developed, there followed a great increase in the number of species, presumably because of the host-specificity that follows the synchronization of the biology of most gall midges with their individual hosts.

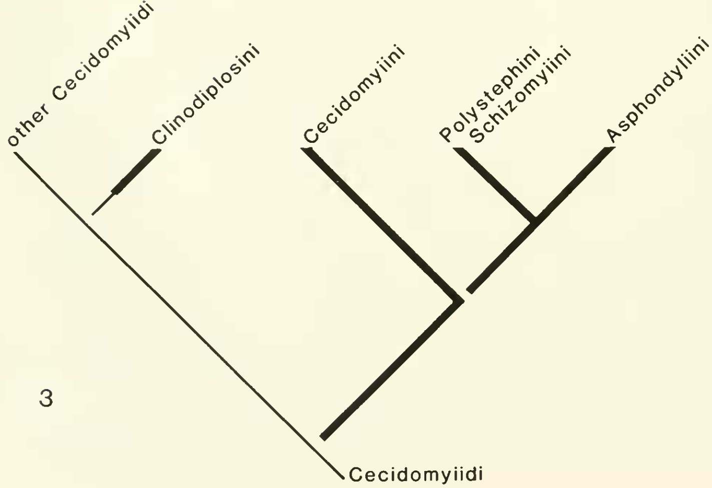
Cecidomyiid larvae are legless, more or less cylindrical, and taper anteriorly to the tiny head, which is much reduced in size compared to that of other Nematocera. Ancestral fungus-feeding Cecidomyiidae developed unique adaptations that preadapted their larvae for plant-feeding. Most of these modifications affected the feeding apparatus of the larvae. The structure of the larval head has been studied in detail by Solinas (1968, 1971). Larvae feed by appressing the cone-shaped head to the food source, exserting the mandibles that pierce and hold fast or scrape the substrate, and immediately discharging salivary secretions. The muscles of the head capsule dilate the esophagus and the predigested fluids are ingested. The salivary glands of all cecidomyiid larvae are large relative to their body size (Mamaev, 1975). Ancestral cecidomyiids also evolved a prothoracic dermal structure called the spatula that appears on the last larval instar, sometimes also the penultimate instar. This organ serves to take over the function of digging from the reduced head. In some plant-feeding gall midges the spatula is used for cutting through woody tissue; in others it is lost. Changes in the feeding apparatus of more advanced, plant-feeding cecidomyiids are relatively minor and differ in detail only. As examples, mandibles become modified for various specific uses (Solinas, 1971), intestines become simplified in plant-feeders (Mamaev, 1975), and spatulae are used for purposes besides digging and are often lost.


other Bibionomorpha
Lestremiinae (350)
Porricondylinae (460)
Lasiopteridi (1640)
Cecidomyiidi (2040)
Cecidomyiinae
Cecidomyiidae

1


Brachineurini
Ledomyiini
Rhizomiini
Oligotrophini
Dasineurini
Alycaulini
Lasiopterini
Lasiopteridi

2


other Cecidomyiidi
Clinodiplosini
Cecidomyiini
Polystephini
Schizomyiini
Asphondyliini
Cecidomyiidi

3

Not only must larval salivary secretions of plant-feeding gall midges be specific to stimulate plant growth, but adults must synchronize their emergence, mating, and egg laying with development of suitable tissues by the host plants. Gall midge larvae do not bore into plant tissue. Usually, the female lays eggs on or among plant surfaces, and the larva, upon hatching, crawls to a suitable site, which always involves meristematic tissue, settles, and begins feeding. Spence (1969) and Rohfritsch (1980) have shown that once a larva settles, the body form changes so that the larva can no longer crawl. The plant then grows quickly around the larva, forming a gall.

Two supertribes contain plant-feeding gall midges (Fig. 1). In the Lasiopteridi (Fig. 2) the most primitive tribes are fungus-feeding and species poor. Plant-feeding probably developed once in this supertribe. All four of the plant-feeding tribes occur on a great variety of plants. Many Oligotrophini produce structurally complex galls, although some species produce simple leaf or bud galls. Some Dasineurini live freely in flower heads but most form simple galls: rolled or swollen leaves, swollen buds, and stems. The Alycaulini and Lasiopterini, chiefly stem gallmakers, have regained a relationship with fungi. Their fungal associates begin growth as a white mycelial mass that ultimately surrounds the larval nidus with a black excrescence which, at about the time the gall midge larvae are full grown, forms a cast around the larvae or their tunnels. In some cases the fungus covers a much more extensive area than that occupied by the larva. For example, the larva of *Asteromyia carbonifera* (Osten Sacken) in a leaf blister gall is stationary and the area immediately surrounding its head remains green until the larva is full grown. Many of these Lasiopterini do not appear to feed on the fungus. In fact, some species, e.g. *Asteromyia modesta* Felt, live in leaf blister galls without a fungal associate (Gagné, 1968).

Primitive members of the supertribe Cecidomyiidi, in the branch labeled "other Cecidomyiidi" in Fig. 3, comprise many kinds of general and specific fungus-feeders, as well as species that are predatory on insects and mites, a habit that evolved at least three times in this supertribe. Most Clinodiplosini in the Holarctic Region are polyphagous fungus-feeders, but some appear to be monophagous fungus-feeders and a few feed in and kill plant buds. In the Neotropical Region, however, many species form complex galls and are host specific.

The other plant-feeding Cecidomyiidi are extremely diverse and rich in species and occur on most groups of gymnosperms and angiosperms. Some live freely in flower heads but most form simple and complex galls. One tribe, the Asphondyliini, which occurs throughout the world on certain groups of angiosperms, has regained a relationship with fungi. Unlike most other cecidomyiids, these gall midges insert their eggs directly into the plant by means of a long needle-shaped ovipositor. It is possible that ovipositional fluid from the female initiates gall formation. The larvae move inside their individual cells and evidently feed on the fungus that grows evenly about the interior surface. Plants affected by As-

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Figs. 1–3. Simplified phylogenetic trees of Cecidomyiidae. Thickened lines indicate plant-feeding groups. Breaks in lines indicate that the basal line is paraphyletic to what follows. 1, Subfamilies and supertribes with number of valid species presently known. 2, Tribes of Lasiopteridi. 3, Tribes of Cecidomyiidi.

phondyliini produce galls that are unique among all other cecidomyiid galls in that they have no nutritive cell layer (Ross, 1932).

In summary, the transition from fungus-feeding to plant-feeding required many modifications to adapt gall midge biology to that of plant phenology and physiology, but the basic adaptations, sucking mouthparts, extraintestinal digestion, and spatula, needed to begin the process were already in place. The most important subsequent changes had to occur in the salivary secretions to make the host plant tissue react to feed the larva. Since plant-feeding mechanisms evolved independently several times, one can suppose that the requisite genetic changes were relatively few. The feeding apparatus of gall midges is a development analogous to that of the cephalopharyngeal skeleton of higher Diptera. In both groups those developments were the precursors of explosive evolution.

Acknowledgments

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